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# Female mating adaptations: Salient features and the influence of fertility status

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***Abstract***

*Modern human beings share the adaptive mating strategies of their ancestral predecessors, even though the adaptive environment is a relic of the past. Due to the large parental investment mammalian females must contribute in order to reproduce, women face unique challenges in their quest for reproductive fitness. This review endeavors to address behavioral, strategic, and perceptual shifts in female mating adaptations within the context of the menstrual cycle in order to yield a greater understanding of modern women and the evolutionary basis for behavior.*

*Keywords: mating adaptations, menstrual cycle, ovulation, ovulatory shift hypothesis, parental investment, ornamentation*

## Introduction

Evolutionary psychology posits that modern day humans are similar in many ways to their ancestral predecessors, and involves the application of evolutionary principles to the study of the evolution of mind (Campbell, 2013). Although the society and culture of modern humans differ considerably from the environment our ancestors inhabited, the challenges those ancestors faced exerted substantial influence on behavioral concepts and adaptations that remain salient today. Theoretically, the environment of adaptation repeatedly presented the same problems, resulting in selection for those abilities that were most advantageous in solving them. Today, curiosity about the differences between male and female behavior has spawned research that focuses on differential properties of male and female humans, primates, and mammals. A core concept that underlies the contrasting behaviors of the sexes is mating: the strategies one uses to acquire a mate, the parental investment each parent must contribute, and the ways in which fertility status affects behavior. Female reproductive biology has evolved to incur an extremely heavy parental investment, and thus selects for an equally discerning sexual psychology (Trivers, 1972). Since the period of fertility in human females is brief, a woman's mating adaptations depend upon her fertility status and the menstrual cycle.

## Evolutionary Background

Charles Darwin, best known for his contributions to evolutionary theory, proposed the concept of sexual selection: a derivative of natural selection wherein some individuals have greater reproductive fitness because they are more capable of securing mates (1871). Sexual selection depends on two separate processes: intersexual competition, the ability to attract mates, and intrasexual competition, the ability to compete against or deter other same-sex rivals for access to desirable mates. For example, peacocks display ornate tail plumage since the brightly colored feathers serve to attract peahens, which are evolutionarily adapted to be attracted to such a feature (Buss & Schmitt, 1993). Truthfully, such an adaptation may expose the male to greater risk of predation and thus jeopardize his chances of survival, but

access to mates takes evolutionary precedence in the male's quest for reproductive fitness. Conversely, a stag may employ the use of large antlers to fight and defeat his same-sex rivals in a display of intrasexual competition. The victorious animal is allowed access to the fertile females within the herd. Similarly, Darwin postulated that various mechanisms of sexual selection have influenced human beings in much the same way as other animals. In particular, he considered two adaptations: the male beard and the relative hairlessness of human beings, as phenomena that have been selected for over time (Darwin, 1871).

Parental investment theory suggests that the individual who must contribute a higher investment to reproduce will adopt a more discriminating mating strategy (Trivers, 1972). Indeed, parental investment encompasses many different concepts, all defined as actions that benefit the offspring and increase its chances of surviving at the expense of the parent organism and its ability to invest in other offspring (Trivers, 1972). Human females carry offspring internally for a gestational period of nine months and are also responsible for birth, lactation, and the primary nurturance of the offspring when it is very young. The large investment of energy that females must contribute in order to reproduce limits how many offspring one woman can produce within her lifetime. As a rule, the more time and effort that are directed toward any individual offspring, the fewer offspring will be produced (Campbell, 2013). Therefore, it is wisest to choose a male mate who is able to assist by acquiring resources and contributing quality genetic material to the potential offspring. Clearly, such a mate is not easy to attract, and intrasexual competition means that females must alter their reproductive strategies accordingly.

Although monogamous relationships have become de rigueur in modern Western societies, it is unlikely that monogamy has been the most common (or advantageous) mating strategy throughout history. Our ancestors pursued both short-term and long-term mating strategies, depending on the social context and the various evolutionary advantages that could be conferred from each (Buss & Schmitt, 1993). The adoption of a particular mating strategy is not considered a conscious decision; on the contrary, it functions as an evolutionary mechanism. Buss and Schmitt (1993) discuss the sexual strategies theory in terms of both sexes' costs and benefits that may result from multiple factors involved in pursuing short and long-term liaisons. Due to the high cost of reproduction that the female sex must bear, women are much more likely to pursue a long-term mating strategy.

**The Menstrual Cycle**

The menstrual cycle is distinct to female humans and certain other species of primates. Essential for the production of ova and the preparation of the uterus for a potential pregnancy, the cycle typically lasts for twenty-eight days in fertile females (Campbell, 2013). The ovarian cycle has special relevance to evolutionary theory, and consists of the follicular phase, ovulation, and the luteal phase. During the follicular phase, the ovarian follicles prepare to release an egg. About twenty follicles mature by way of folliculogenesis and compete with each other to become the "dominant" follicle, which matures into the egg. Ovulation is the phase in which the egg is released from the follicle into the oviduct. Before ovulation, a surge in luteinizing hormone (LH) thins the follicular wall and causes the follicle to release the oocyte. The

egg matures into an ovum and is swept into the fallopian tube. Lastly, the luteal phase maintains the fertile uterine environment for a period of time following ovulation. Although the egg bursts from the ovary during ovulation, the follicle stays on the surface of the ovary and becomes a structure called the corpus luteum. The corpus luteum secretes hormones to maintain the thickened lining of the uterus and allow for potential fertilization of the egg. If a pregnancy does not result, hormone levels fall and lead to menstruation after about fourteen days. Lastly, hormonal fluctuations across the cycle contribute substantially to its functioning. Estradiol, the most potent form of naturally occurring estrogen, fluctuates throughout the menstrual cycle. Estradiol concentrations are likely to be higher during phases of the cycle where a female is more fertile (Campbell, 2013). Similarly, progesterone is secreted upon ovulation and continues to increase in concentration throughout the remainder of the cycle.

**Ovulatory Shift Hypothesis**

Since the period of fertility in human females is very brief, women must maximize opportunities to acquire good genes for a potential offspring (Campbell, 2013). Thus, it may not always be advantageous to adopt a monogamous mating strategy across all phases of the ovulatory cycle. Indeed, there are special circumstances in which the overall sex-specific mating trends do not apply; women may pursue short-term strategies in order to acquire beneficial genetic material that can be passed on to a potential offspring, and there is recent evidence of this pattern of behavior (Gangestad & Simpson, 2000). The phenomenon is termed the "Good Genes" hypothesis, and suggests that a female is much more likely to be motivated to adopt a short-term mating strategy when she is close to ovulation and the likelihood of conception is high.

Similarly, there may be behavioral and perceptual shifts during ovulation that affect reproductive outcomes. Researchers have postulated that such shifts serve to increase the probability that beneficial genetic material will be acquired from a mate and applied to a resultant offspring (Gangestad, Thornhill, & Garver-Apgar, 2005a). The "ovulatory shift hypothesis," coupled with empirical evidence, may help demystify female sexual psychology and the psychological effects of ovulation.

**Primates and Humans**

The mating behaviors and strategies of other primate species are occasionally analogous to humans, but there are also significant differences that render them a poor model for human sexuality in general. In particular, ovulation in humans is concealed or partially concealed (Campbell, 2013). In contrast, the fertile phase in nonhuman primates is flagrantly displayed in the form of bright red genital swellings (Robinson, 1982). The swellings serve to signal female fertility to eligible males within the group. Additionally, female apes and monkeys sometimes mate promiscuously in an attempt to conceal the paternity of a resultant offspring. Infanticide is extremely common within primate bands, and results in one third of infant deaths. Infanticide is thus a serious threat to reproductive fitness, and appears to be chiefly caused by nonpaternity (Hrdy, 1979). Therefore, the creation of "ambiguous paternity" is an adaptive mating strategy that may protect females and their offspring (Hrdy, 1979). Furthermore, apes and monkeys are generally only sexually active during the fertile phase of the cycle,

which is not the case among humans, who may engage in sexual behavior during any phase of the menstrual cycle. However, the evolutionary implications of nonhuman primate mating behaviors are numerous, and suggest that the reproductive fitness of nonhuman primate species is dependent on a number of differential attributes and mating strategies (Robinson, 1982). Since the parental investment by females is so large in humans and nonhuman primate species, the corresponding mating psychology becomes more discerning. "Mate choice" is a concept restricted to females, and evidence of female mate choice is present in humans and nonhuman primate species (Robinson, 1982). Additionally, sexual behavior shifts in apes and monkeys are dependent on the ovarian cycle, a finding that corresponds to the ovulatory shift hypothesis in humans (Van Belle, Estrada, Ziegler, & Strier, 2009).

**Female Mating Behaviors in Humans**

It has long been assumed that ovulation was completely concealed in human females, but a growing field of literature suggests that this may not be the case. Female mating behaviors may manifest as ornamentation, differential choice of clothing, and differential use of cosmetics, and function as an attempt to promote reproductive success. It is common knowledge that many trends in cosmetics and fashion purport to enhance youthfulness, beauty, and signs of fertility (Campbell, 2013). Women who are ovulating may employ varying styles of clothing and cosmetics in an attempt to attract mates at a time when it is biologically crucial to do so. Haselton, Mortezaie, Pillsworth, Bleske-Rechek, and Frederick (2007) found that changes in fertility status as defined by the ovulatory cycle are observable in female self-ornamentation behaviors. The ornamentation effect is an easily detectable phenomenon that is present in many species, and serves to attract potential mates. Thirty women between the ages of 18 and 37 came to the lab and posed for two separate photographs: one taken on a "high fertility" day, and one taken on a "low fertility" day. The lighting conditions and background of the participant photographs were standardized. Seventeen men and 25 women were recruited as judges, and asked to compare the two participant photographs according to a question: "In which photograph is the participant trying to appear more attractive?" Overall, results showed that women actively engage in ornamentation behaviors when they are close to ovulation and highly fertile, and these behaviors are detectable by unbiased observers (Haselton et al., 2007). However, it is possible that the participants did not try to appear especially attractive when they visited the lab, due to the norms of student dress and the lack of mating opportunities there. Durante, Li, and Haselton (2008) addressed this possible confound by asking participants to come to the lab and draw the outfit they would choose to wear to an imaginary social event that evening. Confederates rated the illustrations on a 9-point scale in order to report how "sexy" and "revealing" the outfit was, and results from the high-fertility session conferred higher ratings across both measures. Similarly, participants who were close to ovulation drew outfits that showed more skin, and those results extended to both single and partnered women.

Cosmetics also represent a female attempt to embody youthfulness and beauty, and numerous products are designed to enhance characteristics associated with femininity and fertility, including large eyes, flushed cheeks, and full lips. Makeup is also used to correct facial asymmetries and signal

sexuality (Campbell, 2013). A study by Nicolas Gueguen (2012) postulated that women's behaviors change across the menstrual cycle; more specifically, women who are closer to ovulation invest more heavily in their appearance and thus exhibit greater usage of cosmetics. The study design included one measure conducted in the laboratory, and one in the field (in clubs and bars on a weekend night). In the laboratory environment, participants reported the amount of time they had spent putting on makeup, and two professional makeup artists evaluated participants' usage of cosmetic products. When the participant was close to ovulation, the level of cosmetic usage was higher and the application of a higher quality. In the field, confederates estimated that the level of cosmetics usage was higher (Gueguen, 2012). Though it may not be a conscious decision, it is clear that females alter their behavior during the follicular phase of the ovarian cycle, and the theme extends to consumer behavior, namely the consumption of food and beauty products. Saad and Stenstrom (2012) found that women spend more time, money, and effort on beautification during the fertile phase of the cycle. Participants in the study were asked to track their purchases and answer survey questions about food cravings, clothing items, and cosmetic usage each day for 35 days. The researchers hypothesized that food expenditures would be highest during the luteal (non-fertile) phase, and that appearance related efforts and expenditures would be highest during the follicular (fertile) phase of the cycle. Both hypotheses were fully confirmed by the results (Saad & Stenstrom, 2012). Mating and behaviors related to the acquisition of a mate appear to take precedence over other seemingly basic drives during ovulation. The period of fertility in female humans is fleetingly brief, and thus heightened intrasexual competitiveness and the adoption of mate-attracting strategies are potentially highly advantageous to females during the follicular phase.

**Mating Preferences**

Research literature has identified shifts in female mating preferences across the menstrual cycle, and hormones may exert considerable influence on these effects. In particular, changes in estradiol concentrations have predicted changes in female preferences for facial cues of high testosterone. Women are more highly attracted to facial cues of high testosterone when they are most fertile, and estradiol concentrations also predict the magnitude of the shift in females' preferences (Roney, Simmons, & Gray, 2011). Since estradiol peaks near ovulation, it may act as a moderator of attraction to cues of high testosterone. If high testosterone signals high levels of heritable fitness as theorized, it would be vitally important that females be able to discern the presence of such characteristics in a potential partner in order to acquire beneficial genetic material for an offspring (Roney et al., 2011). It stands to reason that attraction to androgen-dependent cues would be highest during the fertile phase of the menstrual cycle, since that brief period is the only time females are physically capable of conceiving. The effect of estradiol as a moderator of attraction to fitness cues has also been demonstrated in studies on other animals, including rodents (Xiao, Kondo, & Sakuma, 2004) and songbirds (Maney, Goode, Lange, Sanford, & Solomon, 2008). Mating preferences in humans are thought to exist in order to perpetuate evolutionary indicators of genetic fitness in both sexes. The "good genes" approach posits that traits females prefer are viable indications of genetic quality in males, and specific indicators of genetic

fitness in men include facial symmetry, physical strength, social dominance, and intrasexual competitiveness (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007). A masculine face signals other advantages too; men with masculine faces tend to be healthier, less vulnerable to disease, and physically stronger (Little, Jones, & Debruine, 2011). A man who possesses such attributes typically has high levels of testosterone and utilizes a short-term mating strategy. Females who are close to ovulation are more likely to prefer a mate who is highly masculine, since the likelihood of conception is high during the fertile phase of the cycle (and so is the desire to acquire good genes for an offspring). In particular, facial symmetry is a strong indicator of genetic fitness and developmental stability. Women who are pair-bonded to men with symmetrical faces report an increase in in-pair desire when they are close to ovulation (Gangestad et al., 2005b). Conversely, women who are in relationships with asymmetrical men report the opposite: an increase in extra-pair desire during the fertile phase of the cycle. It is probable that this effect occurs because females coupled with asymmetrical men are interested in securing better genetic material than their current mate is capable of offering. The majority of the literature on mating preferences across the ovulatory cycle concludes that in a short-term mating context, females are more likely to be attracted to dominant, charismatic men during ovulation. However, such men are also unlikely to invest heavily in a potential offspring, and the strategic pluralism argument assumes that a female must choose between good genes and paternal investment (Gangestad & Simpson, 2000). Evolutionarily speaking, how do women justify their attraction to a "sexy cad" who subscribes to a short term mating strategy? Strikingly, there are changes in female perception that may influence mating preferences. Durante, Griskevicius, Simpson, Cantu, and Li (2012) asked participants to evaluate photographs and short profiles of "sexy men" and "reliable men" during periods of high fertility and low fertility. Participants were also asked to estimate how much each man would invest in a potential offspring. Paradoxically, women who were ovulating rated the "sexy" men as more likely to be good fathers (Durante et al., 2012). Thus, it appears that ovulation may serve to alter female sexual psychology in ways that promote short-term mating during the fertile phase of the menstrual cycle.

**Mating Strategies and Motivations**

Ancestrally, women who couldn't secure a mate who had good genes and subscribed to a long-term parental investment strategy may have benefited from extra-pair mating strategies. Women's extra-pair desires vary across the ovulatory cycle, and tend to be highest near ovulation, when conception is likely and genetic benefits may be obtained. Haselton and Gangestad (2006) asked 35 women to provide daily self-reports of sexual feelings and interests. When participants were close to ovulation, they reported greater interest in social contexts where the likelihood of meeting men was high. Furthermore, women in relationships reported greater extra-pair flirtation in the fertile phase of the cycle, much to the chagrin of their partners (Haselton & Gangestad, 2006). These shifts in desire provide further support for the good genes hypothesis. Similarly, Bullivant, Sellergren, Stern, Spencer, Jacob, Mennella, and McClintock (2004) hypothesized that female sexual motivations vary across the cycle, and noted that the link between ovulation and sexuality is often obscured by imprecise measures of fertility. To identify ovulation

in participants, the researchers measured the surge in luteinizing hormone (LH) that immediately precedes the onset of ovulation and related it to reported changes in sexual activity. Participants in the study were much more likely to be sexually active and to initiate sexual activity in the days before and during the LH surge, indicating that ovulation has a substantial effect on women's sexual desires and motivations (Bullivant et al., 2004).

**Involuntary Physiological Responses**

Human female mating behaviors, perceptions, and motivations fluctuate with respect to the ovulatory cycle. Researchers measure the majority of these phenomena through the use of questionnaires, self-reports, and ratings of photographs (Laeng & Falkenberg, 2007). However, each of these methods is inherently limited due to the conscious introspection and verbal expression that is necessary in order for a participant to report. Pupillometry, the measurement of the diameter of the pupil, constitutes a measurable physiological variable that is both involuntary and related to the level of interest produced by a particular stimulus. Laeng and Falkenberg (2007) predicted that the menstrual cycle would affect pupillary size in the seven participants who were not using hormonal birth control. Fourteen participants viewed 20 photographs, including images of famous actors of the same and opposite sexes, Norwegian celebrities, other participants' boyfriends, and the participant's own boyfriend. The maximum increase in pupil size was displayed when participants were close to ovulation and viewed photographs of their boyfriends. Indeed, the perceived attributes of the participants' boyfriends were twofold: they represented both sexual interest and attainable reproductive possibility, and the latter is of heightened significance during the fertile phase of the cycle. Also of note is the effect of hormonal birth control on the findings: the seven participants who were using hormonal birth control did not show fluctuations in pupil size in relation to the menstrual cycle, which suggests that the "pseudo pregnancy" induced by hormonal contraception is effective in inhibiting normal cyclic fluctuations in pupillary responses to stimuli. Overall, female mating behaviors are generally highly visible and thus easily observable by others. Far more complex are the shifts in cognition that may be responsible for female mating preferences and strategies as they near fertility (Campbell, 2013). The covert nature of these shifts means they present a greater challenge to researchers, and unique research methodologies have been introduced in an attempt to reveal the subtle aspects of female attitudes and preferences with respect to the ovulatory cycle.

**Discussion**

Indeed, study results must be considered alongside limitations present in the research. The most recurrent issue that arose is one that affects the majority of psychological research as a whole, since the undergraduate student population is easy for researchers to sample from. Virtually all of the participants in the ovulation studies that were reviewed were undergraduates from the United States. Sampling from universities is convenient, but limits the generalizability of results to other cultures, social contexts, and age groups (Stanovich, 2012). A second problem was the occasional inaccuracy of one of the methods used to predict fertility: the reverse cycle count. The reverse cycle count method is based on a 28-day cycle, which some women may deviate from (Haselton & Gangestad, 2006). Furthermore, this method relies on the

participant's self report of the last onset of menses, and is thus less accurate than measuring hormone levels.

Research on ovulation has yielded a wealth of information about behavioral changes that occur during the fertile phase of the cycle. However, little is known about the changes in cognition that may underlie the explicit, observable behaviors. For example, a woman may feel more attractive during ovulation, leading her style of dress to change and appear more risqué than it would normally. She may also have a stronger urge to behave in ways that make her more sexually competitive. Thus, it is crucial that researchers continue to employ unique experimental designs in an attempt to isolate the cognitive effects of ovulation An additional avenue for future ovulation research could be the impact of ovulation on other individuals. The majority of the current literature focuses solely on the changes in the ovulating female and not the reactions of others, although in some studies males have been found to guard their mates more closely during ovulation (Pillsworth & Haselton, 2006). In particular, it may be fruitful to examine the responses of other women (peers) and family members (kin). For example, are other women capable of detecting ovulation in their peers? If so, do they perceive the fertile female as a competitive threat? Are family members affected by the ovulation of a fertile female? A possible prediction: fathers may be more protective of their daughters during the follicular phase, to ensure that she is only investing in long-term relationships that are likely to be advantageous to her in the future.

Some of the most compelling research inquiries of the past decade have found links between female mating adaptations and the menstrual cycle, and numerous studies have elucidated the menstrual cycle's effects on female behavior, sexuality, and sexual psychology. In particular, the field of evolutionary psychology has shed light on why ovulation might have these effects on females, and what advantages they might contribute to an individual's reproductive fitness. Evolutionary psychology teaches that much of present behavior is a function of past adaptive success, and offers the hope of integration in the understanding of human behavior.

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